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THE DYNAMIC FINE ROOTS OF FOREST TREES

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Abstract

Fine roots represent a dynamic portion of the total below-ground biomass of forest trees. As demonstrated in recent research, fine roots are in constant flux with death and replacement taking place simultaneously. Data on the temporal variations of fine-root death and replacement are given from a young 20-year-old and a mature 120-year-old Scots pine (Pinus sylvestris) stand in Central Sweden. Two methods were used to investigate fine-root dynamics: (i) By means of data obtained from sequential core sampling and (ii) measurement of the ingrowth of new roots into root-free cores removed at regular intervals. Both methods gave fine-root production estimates of similar magnitude. The young stand had proportionately more dead fine roots than the mature stand. An annual carbon budget for a 14-year-old Scots pine reveals that roughly 60 % of the total net photosynthetic production is invested in the growth and maintenance of the root system. Some general working hypotheses are generated from the available data for future work on root dynamics.

INTRODUCTION

Forest trees, like other living organisms, are composed of many functional parts essential to the well-being of the whole organism. How much a forest tree may grow is ultimately determined by the amount of foliage it can support and the activity of its root system. The general vigour of the tree is to some extent reflected by the accumulated amounts of carbohydrates. From investigations of the seasonal changes in the starch reserves of various organs (needles, roots etc.) it is recognized that these fluctuations are determined by the growth and carbohydrate dynamics of the whole tree (cf. Ericsson & Persson 1980). However, the food supply is normally not the limiting factor as regards root growth, since carbohydrate reserves are usually to be found in large amounts in root tissues throughout the growing season.

What controls the death and replacement of fine roots in forest ecosystems is a matter of conjecture (Caldwell 1979, Hermann 1977, Lyr & Hoffman 1976, Persson 1981b, 1982, Sutton 1980). Methodological difficulties, i.e. lack of uniform investigatory techniques together with varying environmental conditions make it practically impossible, at present, to draw general conclusions from available data in literature. During recent years, many authors have come to the conclusion that growth in the root systems occurs relatively independently of growth in above ground parts and that the temporal variation is largerly determined by changes in environmental conditions. Most authors share the opinion that the factors determining root growth are complex and involve environmental conditions of both above and below-ground plant parts, nutritional status, carbohydrate supply and allocation in the plant, respiratory costs, growth regulatory substances (root hormones), and genetic influences (cf. i.e. Deans 1979, Ericsson & Persson 1980, Farrell & Leaf 1974, Fogel 1980, Fogel & Hunt 1979, Hermann 1977, Keyes & Grier 1981, Kimmins & Hawkes 1978, Persson 1980c, 1982, Reynolds 1970, 1974, Safford 1974, Santantonio 1979, Santantonio et al. 1977, Torrey 1976, Trappe et al. 1977, Vogt et al. 1980, 1981). Furthermore, in a forest stand, and in forest trees competition between individuals of the same species and interspecific competition between different plant populations influence the process of root growth.

Most works on the temporal pattern of fine root growth of boreal forest trees indicate considerable variations in fine roots during the growing season (Deans 1979, 1981, Ford & Deans 1977, Göttsche 1972, Grier et al. 1981, Harris et al. 1973, Harris et al. 1977, Harris et al. 1980, Heikurainen 1955, Kalela 1955, Kohman 1972, McClaugherthy et al. 1982, Persson 1978, 1980a, 1980b, 1980c, 1981a, 1982, 1983a, 1983b, Roberts 1976). Fine roots are in a state of constant flux, with death and replacement often taking place simultaneously and although there is growing evidence of large fluctuations occuring in fine roots length and biomass, there are few estimates of their rates of production and turnover.

Fine roots exert a significant influence on soil profile development and, upon dying, they contribute substantially to the organic matter content of soil (Coleman 1976, Head 1973, McClaugherty 1982, Persson 1979b, 1982). Thus, much fine-root biomass is constantly being transformed into necromass (dead fine-root tissue), frequently not estimated or accounted for in turnover calculations. Fine-root necromass may vary considerably during the growing season (Head 1973, McClaugherty et al. 1982, Persson 1978, 1979b, 1980a, 1980b, 1980c, 1981a, 1982, Reynolds 1970, Santantonio 1979, 1982, Santantonio et al. 1977). Together with litter from the aerial parts of plants, shedded roots provide the main bulk of material for the complex decomposition cycles that occur in the soil. These include bacteria, fungi and soil animals (cf. Vitousek 1982, Persson, T. et al. 1980).

METHODS USED IN THE STUDY OF FINE-ROOT PRODUCTION

Numerous investigations of tree root systems in boreal forests have been based on excavations of root systems of complete trees. Small-diameter roots as well as mycorrhiza are usually omitted since detailed excavations of entire root systems would be too time-consuming and great difficulties are involved in extracting roots from even small soil-samples. Because of the methodological difficulties involved in studying root systems, dynamic aspects have been largely neglected.

The simplest way of studying the periodic changes in fine roots is from volumetric soil samples which reflect the standing crop (biomass and necromass) throughout the year. This method is however, best on sandy forest soils where the soil is easily penetrated. The excavation of large soil blocks (monoliths) is currently the only feasible method on till soil. Quantitative data on fine-root dynamics of forest ecosystems on till are therefore presently conspicuous by their absence.

Two methods were used within the Swedish Coniferous Forest Ecosystem Project (SWECON) to investigate fine root dynamics: (1) using data obtained by sequential core sampling and (2) measuring the ingrowth of new roots into root-free cores (ingrowth cores) removed at regular intervals (Ericsson & Persson 1980, Flower-Ellis & Persson 1980, Persson 1978, 1979b, 1980a, 1980b, 1980c, 1981a, 1982, 1983a, 1983b). The ingrowth method consists of removing a core and refilling the hole with sifted soil containing no roots. Thus, the core initially consists of cylindrical 'net stockings' filled with sifted sand. The core is then resampled after a period of time and the root that have grown into it are measured.

Most root studies hitherto conducted in forest ecosystems generally fail to characterize where and when the root growth takes place. Existing published data have the following limitations: (1) sampling has been carried out at a few intervals during the growing season, (2) the fine-root biomass includes an unknown amount of dead roots, (3) the dead fine-root fraction (necromass) was not estimated, (4) the number of replicate samples was insufficient to detect significant differences between samplings. (5) the estimated quantitative variables (e.g. the number of root tips, root length etc) are not directly convertable into changes in root weight (6) the root sampling was not carried out on an area basis and (7) the root fragments were not classified into species or diameter-fractions.

Similar criteria, in order to distinguish live fine roots from dead ones, have been elaborated by different workers i.a. McClaugherty et al. (1982), Persson (1978), (1980a), (1980c), (1981a), (1982), (1983a), (1983b), Santantonio (1979), (1982), Santantonio et al. (1977). Living rootlets are far more resilient than dead ones and are not so easily broken if twisted or bent. Actively growing root tips are light-coloured, succulent and unsuberized. Dead rootlets are often wrinkled and dark in colour, fine ramifications are often shed and, if resistant, easily broken off. When it is difficult to see whether a root-fragment is living or dead, it can be determined by the degree of cohesion between the cortex and perioderm. The rootlets are then cut lengthwise with a sharp dissecting knife and the section surface is examined under a stereo microscope (Persson 1978, 1980a).

A number of different research workers have estimated fine root production by adding increments in the fine-root biomass only for an annual period without estimating the dynamic changes in the dead roots. This assumes that death and replacement of fine roots do not take place simultaneously since root mortality is ignored (e.g. the accumulation of fine root necromass in the soil). Only a few workers (see literature above) have so far incorporated the dynamics of dead fine root into their calculations. A correction for overestimation is necessary in all these calculations, if only increments (or decrements) are added, cf. Persson (1980a). At present all net primary production estimates of fine roots are fairly conservative, e.g. they indicate the lowest possible values.

The ingrowth method (see above) can be used to estimate annual fine root production, from the amount of new roots in the cores during a period of one year. The estimate is then calculated as the difference between the highest and lowest estimate during an annual period. Both living and dead root ramifications can be included the calculation.

RECENT DATA ON THE ROOT DYNAMICS OF FOREST TREES

During recent years, new information on the growth dynamics of fine roots has been obtained by the root studies performed by the author as a part of the

Swedish SWECON Project, Ågren et al. (1980), Ericsson & Persson (1980), Flower-Ellis & Persson (1980), Persson (1978), (1979b), (1980a), (1980b), (1980c), (1981a), (1982), (1983a), (1983b). A general summary of these studies is given below.

The root systems of forest trees extend horizontally into new, unexploited areas by means of fast growing lateral roots. The lateral roots in a forest stand grow over and into one another, forming an integrated network of expanding root systems. Coarse-diameter roots (> 2 mm in diameter) are more frequently found near the tree stems and a gradual decrease in mean diameter is generally observed towards the periphery (Fig. 1). The coarse roots are, furthermore, fairly irregularly distributed in the soil horizons, resulting in a fairly irregular occurrence in the core samples, while sampling in a forest stand. The fine roots (< 2 mm in diameter), on the other hand, have a fairly uniform distribution in the tree stand, unrelated to their distance from the nearest tree (Fig. 2).

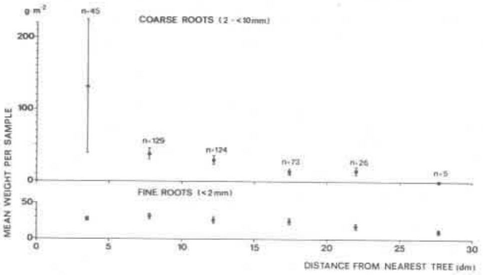

Fig. 1. The horizontal distribution of the coarse and fine roots of Pinus sylvestris in relation to the distance to the nearest tree. Estimates are given as mean biomass ± one standard error (g DW m^{-2}) in 0.5 m intervals from the nearest tree (n = number of samples in each intervals). The estimates are projected in the diagrams at the mean distance in each interval.

Fine roots represent a large and dynamic portion of the total below-ground biomass of forest tress. Results from the SWECON Project indicate that 52, 96 and 78 % of the root weight, surface area and length, respectively (< 10 mm in diameter) in the young stand (Ih II) and 39, 97 and 80 % in the mature stand (Ih V) consist of fine roots (< 2 mm in diameter). In the root fraction (< 1 mm in diameter) in particular there is to be found a rather substantial population which on an average is < 0.5 mm (Fig. 2). The root weight in diameter fractions greater than 1 mm in diamter is to a varying degreee dependent on the accumulated biomass in the woody structures.

One surprising result of the present root study is the large flux of organic matter which is involved in the fine root dynamics. Large variations in fine root biomass (FRB) and fine root necromass (FRB) are to be found in both stands (cf. Fig. 3). During stand development the fine roots represent a varying proportion of the total root weight (Fig. 3). The overall level of fluctuations in FRB was considerbly lower in Ih II than in Ih V - the pooled average of FRB in Ih II was only 0.2 times that in Ih V. The related FRN fluctuated, however, at nearly the same level in both stands, probably indi-

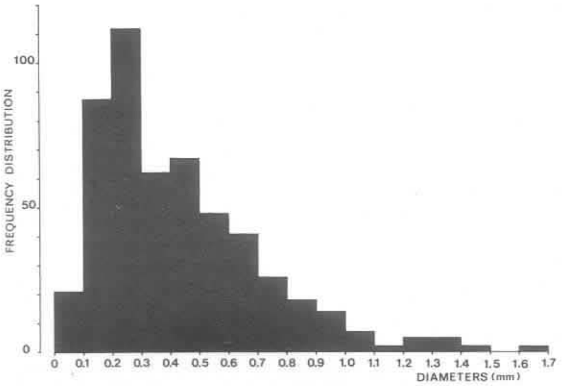

Fig. 2. Frequency distribution of *Pinus sylvestris* fine roots in the < 1 mm diameter-class during the year of sampling 1974-75. The histogram has been derived from 20 diameter samples taken on each sampling occasion in each one of two strata.

cating a larger annual supply of dead roots to the soil in Ih II (Fig. 3). The overall levels of FRB and FRN (Table 1) are relatively low compared with other structural tree components cf. Albrektson (1980a), (1980b), Axelsson (1981), Flower-Ellis et al. (1976), Flower-Ellis & Olsson (1978), Flower-Ellis & Persson (1980). Thus, FRB accounts for a small portion of total tree-root biomass, including the coarse roots and stumps, since much of the root biomass accumulates in the latter structures.

In the young stand, the tree root systems are still expanding, both horizontally and vertically and new soil volumes are successively occupied (cf. Persson 1980a). Because of the varying ratios of live to dead fine roots, it was judged as more correct to relate the estimates of the fine-root production (Table 1) to the average fine root biomass + necromass *viz.* the standing crop of the fine roots. The fine-root production estimates in the different soil environments are, probably, closely related to the degree of exploitation by the different root systems.

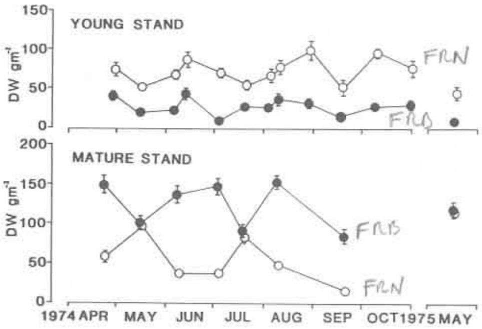

Fig. 3. Variation in the fine-root biomass (FRB) and fine-root necromass (FRN) of *Pinus sylvestris* in a young stand (Ih II) and in a mature stand (Ih II). Estimates are given as means ± standard errors. FRB and FRN = < 2 mm in diameter.

The magnitude of the fine-root production estimates, calculated from the sum of increments in FRB or in FRB+FRN (see methods of calculation in Persson 1978, 1980a) were confirmed by data obtained from the ingrowth experiment. Thus, since the death of fine roots was proportionally low during the 1975-76 growing season and the ingrowth of new roots took place fairly rapidly, the accumulated standing crop in the cores must be considered as an indication of the annual below-ground production. Note, however that the sequential core sampling series were obtained during the growing season 1974-75. The two sets of estimates, from the sequential core sampling series (Table 1) are not strictly comparable, since the number of samplings differed (13 in Ih II and 8 in Ih V, during the growing season 1974-75).

The differences in the growth strategies of the fine roots in the two stands become even more pronounced when one regards the number of root tips per cm fine roots (Fig. 4). The average number of root tips per cm was as much as 2.8, 1.8 and 2.2 in the F/H layer, the mineral soil and the total soil profile down to 30 cm in Ih II. The related estimates in Ih V were 1.5, 0.7 and 1.3, probably reflecting differences in the mycorrhizal development. This difference in the growth strategies may also apply to the soil profile, which is characterized by a heavily ramified net-work of mycorrhizal fine roots in the F/H layer and formation and elongation of fast growing long roots in the mineral soil (cf. Persson 1980a).

An annual carbon budget of a 14-year-old Scots pine is summarized in Fig. 5. It indicates that roughly 60 % of the total net photosynthetic production is invested in fine root growth and respiration. The annual utilization of carbon was distributed between respiration (10 %), stem growth (9 %), branch growth (8 %) current needle growth (17 %) and fine root growth (57 %). All these values were estimated from independent measurements (cf. Ågren et al. 1980). Although considerable uncertainties may exist in some of the components of the carbon budget, it surprisingly well-balanced.

The values for the below-ground production used for the calculations of the carbon budget should be regarded as minimum estimates of the absolute magnitude. With an increasing number of samplings there is an increased chance of measuring extreme figures, - i.e. 'local' minima and maxima - which would affect the productivity estimates. The sampling frequency employed (every 2

Table 1. Pooled average standing crop of the fine roots (FRB + FRN = < 2 mm in diameter) in a young Scots pine stand (Ih II) and in a mature Scots pine stand (Ih V) during the 1974-75 samplings. Also given are the below-ground fine root production calculated from either the sum of increments of FRB or FRB + FRN and the ingrowth of new roots into root-free cores (ingrowth cores) removed on successive sampling occasions. For original data see Persson (1978); (1976b); (1980c); (1983a) and (1983b).

Area	Average FRB+FRN 1974-75 (g DW m^{-2})	Fine-root production (g DW m^{-2} yr^{-1})	
		Increments in FRB or FRB+FRN 1974-75	Ingrowth 1974-75
Ih II	139 ± 80	183 ± 16	139 ± 80
Ih V	128 ± 31	159 ± 29	128 ± 38

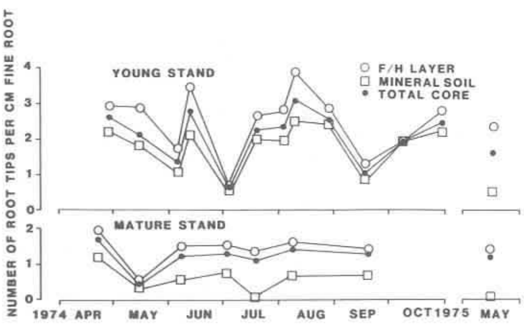

Fig. 4. Seasonal fluctuations in the number of root tips per cm fine root (< 2 mm in diameter) in Ih II and Ih V. Circles = F/H layer, squares = mineral soil down to 30 cm; filled circles = the whole profile down to 30 cm.

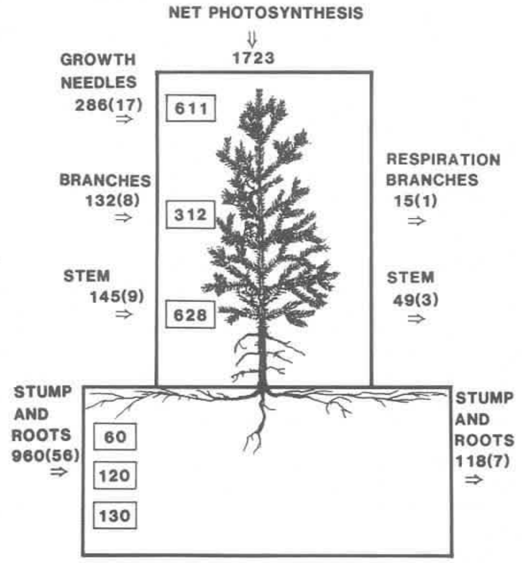

Fig. 5. An annual carbon budget calculated for a 14-year-old Scots pine. For original data see Ågren et al. (1980) and Persson (1978).

weeks in Ih II, every month in Ih V during the growing season) seems to have covered major fluctuations but probably not all the changes which occurred. Growth which took place during the winter months (November 1974 - April 1975) was not estimated, since sampling could not be undertaken in the frozen ground.

FINE ROOT DYNAMICS OF FOREST TREES - AN OUTLINE FOR FUTURE STUDIES

Past investigations of forest production virtually ignored the important role of fine roots and mycorrhizae in carbon and nutrient cycling. Research into tree growth was usually concerned with the above-ground parts of the tree, since these structures provide economically important tissues (i.a. tree stems). The growth of trees, like all perennial species, involves the transfer of dead organic tissues (e.g. foliage and fine roots) from the tree to its environment. The fine roots share of the total organic material that is supplied to the soil is substantial. In this context, the root studies within the SWECON-project have provided new information on the importance of the large supply of dead roots to the soil for the complex decomposition cycles (cf. T. Persson 1980).

Although~~,~~ most existing fine root studies are of a preliminary nature, some general working hypotheses may be generated for the future work on root dynamics from the present knowledge:

i. The carbohydrate supply does not normally limit root growth; most forest plants are generalyy able to invest a considerable amount of energy during the year into fine root growth (and to some extent into mycorrhiza) from a relative carbohydrate surplus. The occurrence of mycorrhiza on forest tree roots should probably be regarded as a result of the latter carbohydrate surplus.

ii. The ion and water uptake in dry forest soil, when it is partially wetted is confined to a zone of the new roots immediately behind the apex of the root tips. The latter zone is generally short-lived in its effectiveness, since suberization occurs rather soon and local depletion of nutrients takes place around the root tips, therefore they must continually be renewed.

iii. The whole soil profile is most efficiently exploited by the root systems. Growth is then promoted in soil horizons where they experience the best water and nutrient conditions. If the quality of the soil is poor (e.g. in the mineral soil), there is a tendency for the tree root system to develope long roots which penetrate large soil volumes rapidly. On the other hand, if the soil conditions are better (e.g. in the F/H layer) the development of ramifications with numerous short roots (e.g. mycorrhiza) is promoted, leading to an exploitation of available moisture and nutrients.

iv. The root dynamics differ along a moisture gradient from one forest stand to another. A wet forest stand has more living than dead roots (average live/average dead > 1) and the opposite holds for a dry stand. The major influence of increased soil moisture is to improve the decomposition and mineralization of dead roots so that the flux of critical nutrients in the soil is increased.

v. Fine-root production may vary substantially from one year to the next. The latter differences may be even more substantial than the differences between sites. There appears to be as much variation in fine-root dynamics within as between species.

At present, we have to admit that relatively little is know of the mechanism controlling root growth and the range of fine root production in forest ecosystems. We may have enough observations from available field experiments to generate working hypotheses, even if they may be modified, as further information is obtained from field and model experiments. Solid knowledge is however scarce. The need for further research in this particular field of root biology is evident.

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